CHANGES IN FIRING RATE
OF HUMAN MOTOR UNITS DURING LINEARLY CHANGING
VOLUNTARY CONTRACTIONS

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SUMMARY

1. Human subjects generated approximately linearly increasing or decreasing voluntary, isometric contractions using the first dorsal interosseus muscle of the hand.

2. Single motor units began firing at $8 \cdot 4 \pm 1 \cdot 3$ impulses/sec (mean $\pm$ S.D. of an observation) and increased their firing rate $1 \cdot 4 \pm 0 \cdot 6$ impulses/sec for each change of 100 g in voluntary force. These values were independent of the threshold force for recruiting motor units.

3. At intermediate rates of increasing and decreasing voluntary force (one complete cycle every 10 sec) the firing rate of single motor units varied linearly with force over the entire range of forces studied. However, during slow increases in voluntary force, the firing rate tended to reach a plateau, while during rapid increases an initial train of impulses at a roughly constant rate was observed.

4. The relative importance of recruitment and increased firing rate, as mechanisms for increasing the force of voluntary contraction, was determined. Only at low levels of force is recuitment the major mechanism. Increased firing rate becomes the more important mechanism at intermediate force levels and contributes the large majority of force if the entire physiological range is considered.

INTRODUCTION

In their initial study on single human motor units, Adrian & Bronk (1929) noted two mechanisms whereby the force of a voluntary contraction could be increased. Either the number of active motor units could be increased, which is known as *recruitment*, or the rate of discharge in the motor units already active could be increased. This second mechanism

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is often referred to as *frequency coding*, but we will use the term *rate coding* for the reasons discussed by Partridge (1966) and Mannard & Stein (1973).

Although they described both mechanisms, Adrian & Bronk (1929) were struck by the analogy of the rate coding found in motor units to that in sensory neurones, and tended to emphasize this mechanism as the major one for increasing force during reflex or voluntary contractions. More recent work has tended to emphasize recruitment. Indeed, several workers found very little increase in firing rate except near the threshold at which motor units were activated reflexly by a linearly increasing muscle stretch in animals (Granit, 1958; Grillner & Udo, 1971), or by voluntary activation in man (Bracchi, Decandia & Gaultierotti, 1966) The firing rate appeared to be stabilized over a wide range of forces, although it might increase again during nearly maximal voluntary effort (Bigland & Lippold, 1954; Kaiser & Petersén, 1965; Clamann, 1970). Rate coding has, therefore, been relegated to a lesser role, functioning perhaps for fine control at low force levels, and during the strongest contractions as well.

In the previous paper (Milner-Brown, Stein & Yemm, 1973b), we determined the twitch tensions for a substantial fraction of the motor units in the first dorsal interosseus muscles of three subjects. This was done by averaging the steady discharge of single motor units at just above the threshold force level required to recruit these units. By following the discharge of some of the same units during controlled changes in voluntary contractions at supra-threshold levels, we have measured quantitatively the relative importance of recruitment and rate coding during voluntary, isometric contractions. To our surprise, we found that the results were contrary to the ideas arising from much of the recent work and were closer in many ways to Adrian and Bronk's original view. Some of these results were recently demonstrated to the Physiological Society (Milner-Brown, Stein & Yemm, 1972).

METHODS

Methods for determining the contractile properties of single motor units, and the threshold force at which they are recruited, have been fully described (Milner-Brown, Stein & Yemm, 1973a; Milner-Brown et al. 1973b). In order to examine how the firing rate varied with force, subjects were asked to track triangular wave forms, while recordings were made from a bipolar needle electrode inserted into the first dorsal interosseus muscle of the hand. The triangular wave forms were displayed on an oscilloscope after summing with a square wave which had a high repetition rate (1000 c/s), and an amplitude equal to 6 % of the peak-to-peak extent of the waveform. The summation produced a visual display consisting mainly of two horizontal lines which moved up and down the oscilloscope at a constant rate. The force generated by the subject against a stiff tension transducer (compliance = 0·5 mm/

kg) was displayed on the second beam of the oscilloscope. The subject was asked to press against the force transducer with the lateral edge of his first finger so as to keep the force within the limits set by the horizontal lines. Subjects learned this task readily, and were able to keep the force within the limits most of the time. The range of forces required to track the triangular wave forms was varied from 400 to 1600 g. The base of the triangle was usually adjusted to a level about equal to the passive force of the hand resting against the transducer. The standard cycle time
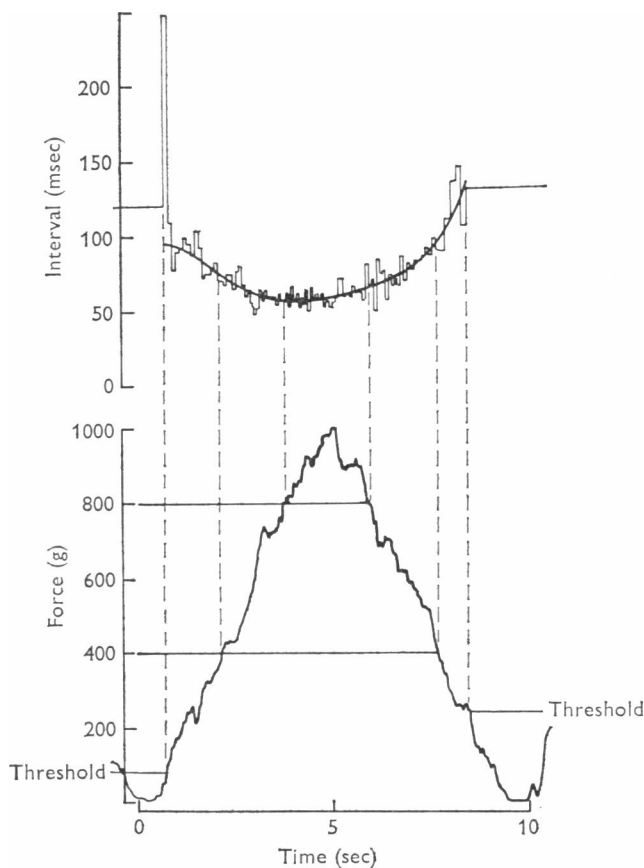

Fig. 1. Continuous record of interspike intervals from a single motor unit (upper tracing) and force (lower tracing) generated by the muscle in tracking a triangular wave form which required 1 kg of effort. The interrupted lines indicate the measurements made, as indicated in the text, at threshold and at predetermined values of force (e.g. 400 and 800 g on the rising and falling phases of the force record). The value of interspike interval plotted on the pen recorder (to an accuracy of $\pm 2 \cdot 5$ msec) is that of the preceding interval, so the last interval before the unit stopped firing is held, and a long interval (> 250 msec) is plotted as soon as the force surpasses threshold and the unit again begins to fire.

(the time for one repetition of the triangular wave form) was 10 sec, but this was varied in later experiments as described under Results.

Signals from (1) a bipolar needle electrode, (2) surface EMG electrodes, (3) the force transducer and (4) a wave form generator were recorded on four channels of an FM tape recorder (see details in Milner-Brown *et al.* 1972). In replaying the signals, each impulse from a single motor unit was used to reset a digital counter after shifting the value of the previous interval into a simple digital-to-analogue converter for display (Stein 1968). Thus, the *duration of the last complete interval* could be plotted, together with the force generated, on two channels of a pen recorder. A smooth curve of interspike interval against time was drawn by eye, and the following measurements were made from the fitted curve (see Fig. 1):

(1) the interspike interval and the force level at which the discharge began (note that by using the fitted curve, we smoothed the records and took into account the first few intervals);

(2) the intervals when the force passed various, predetermined levels on the rising and falling phase of the wave form; and

(3) the interval and force level at which firing ceased on the declining phase of the triangular wave form. Typically about ten wave forms were averaged, and the inverse of the mean interval (mean rate of firing) was computed, together with the s.e. of the mean.

<div align="center">RESULTS</div>

After determining the contractile properties and the threshold force for recruitment of a motor unit as described in the previous paper (Milner-Brown *et al.* 1973*b*), we attempted to measure the variation in firing rate of these units with the level of a voluntary contraction. Subjects were asked to apply sufficient force to track a triangular wave form displayed on an oscilloscope (see Methods). The force actually applied was measured by a stiff transducer and displayed continuously on the same oscilloscope for comparison. Fig. 1 shows a sample of the force applied by a subject in such an experiment, together with a continuous record of the interspike intervals and the measurements made from these records (see Methods).

<div align="center">*Firing rate of motor units*</div>

Fig. 2 shows the averaged data, from over ten triangular wave forms, for firing rate as a function of force during a voluntary contraction. The symbols indicated by (+) represent the threshold values at which the units began and ceased to fire on average. Both units shown began to fire at a slightly higher rate than the rate observed just before they became quiescent (see also Clamann, 1970). This was true for twenty out of the thirty-one units studied; the mean difference was only 0·8 impulses/sec, but this was significantly different from zero at the 1 % level of confidence. The average of the two measurements of threshold rate for all the units studied was 8·4 ± 1·3 impulses/sec (mean ± s.D. of an observation). These values agree reasonably well with the onset intervals (142 ± 39 msec) measured by Petajan & Philip (1969) for this muscle. The mean firing

rate did not depend significantly on the threshold force at which the unit was recruited, although a dependence has been reported in other muscles (Bigland & Lippold, 1954; Clamann, 1970).

Once they became active, both units shown in Fig. 2 increased and decreased their firing rate in quite a linear fashion as a function of the force
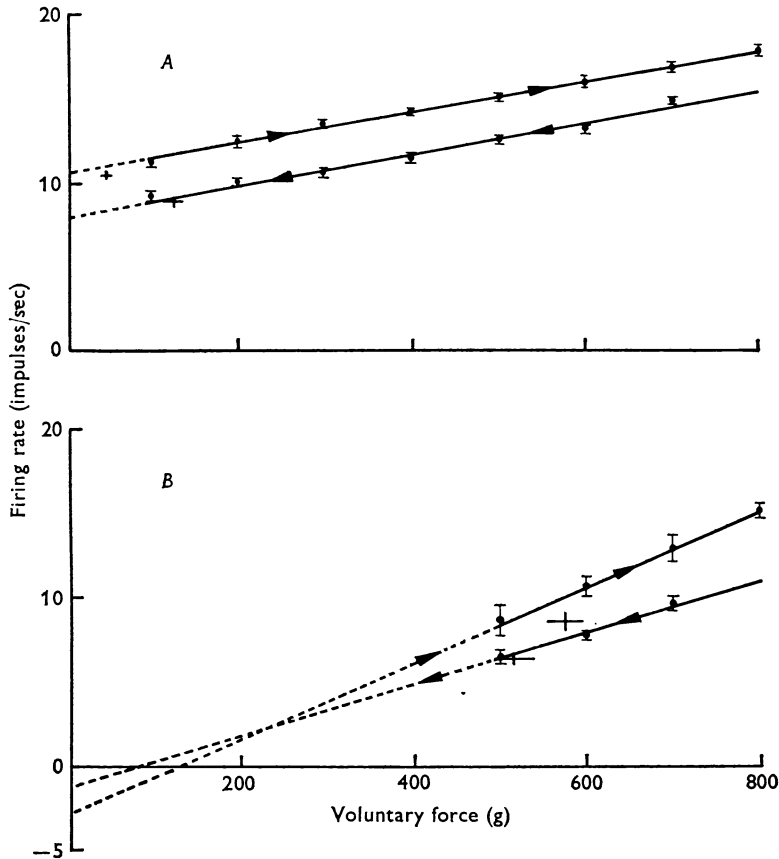

Fig. 2. Firing rate of two motor units at threshold (+) and when passing predetermined force values (✛) during increasing (arrows directed upward to right) and decreasing (arrows directed downward to left) voluntary contractions. The extent of all symbols gives the s.e. about the mean values indicated from tracking over ten cycles of a triangular wave form. The straight lines were chosen to give the least mean square deviation from the data points at the predetermined force values (correlation coefficients all > 0·98). The parameters used to specify these straight lines are the slopes and the firing rates extrapolated back to 0 voluntary force. The firing rates at the intercept cannot, of course, be measured directly, because the units shown ceased firing at a mean threshold of (A) 90 g and (B) 545 g.

generated by the whole muscle. The calculated best-fitting straight lines
are shown in Fig. 2 for the data from the rising and falling phases of the
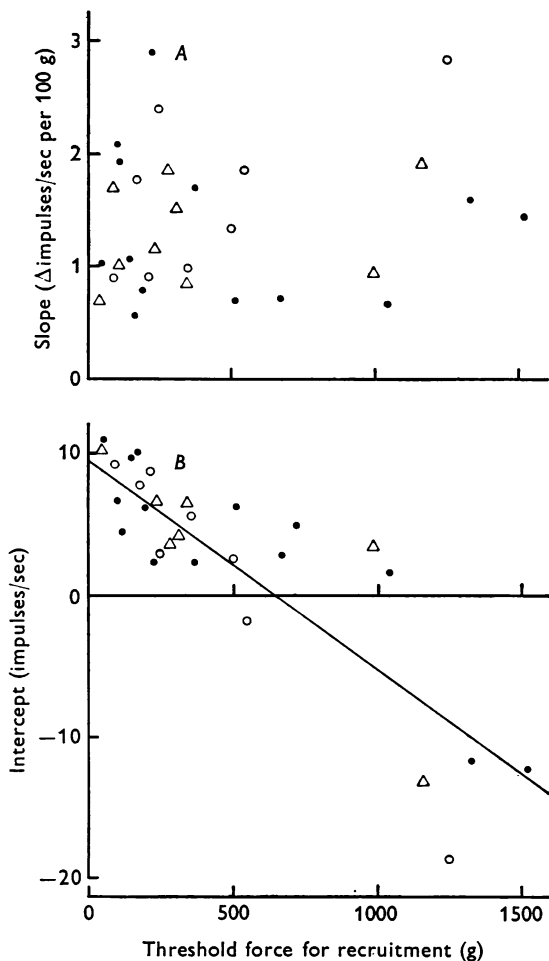tension wave forms. Straight lines typically fitted the data extremely well

Fig. 3. Slopes (*A*) and intercepts (*B*) of best-fitting straight lines (determined
as shown in Fig. 2). Data for thirty-one units from the three subjects
(indicated by different symbols) have been combined. The slopes did not
change significantly with the threshold for recruiting a unit (correlation
coefficient = 0·12), but the intercepts did (correlation coefficient = 0·86).
The implications of this result are discussed in the text.

(linear correlation coefficients were nearly all well above 0·9), though the
best-fitting line for the falling phase was often shifted (Fig. 2*A*) or had a
somewhat different slope (Fig. 2*B*) from that for the rising phase.

These straight lines can be characterized by two parameters:

(1) the slopes, which give the increase in firing rate for each 100 g increase in the force generated by the whole muscle, and

(2) the intercepts, which give the rates of firing extrapolated back to zero force; the region of extrapolation below the first data point for a particular condition is indicated by interrupted lines in Fig. 2. Fig. 3 gives the values of these parameters as a function of the threshold force for recruitment. Although the higher threshold unit in Fig. 2 has a steeper slope than the lower threshold unit, this trend is very weak in general and was not statistically significant. Units with all threshold values tended to increase their firing rate about $1\cdot4 \pm 0\cdot6$ impulses/sec (mean $\pm$ s.d. of an observation) for each 100 g increase in the level of voluntary contraction.

A relation is seen (Fig. 3*B*) between the intercepts and the threshold level of voluntary force required to recruit a motor unit. As indicated in the Discussion, this relationship suggests that rate coding becomes increasingly important at higher thresholds. This hypothesis will be examined in detail later (see *Recruitment vs. rate coding*), but first we must consider how the firing rates depended on the speed of contraction, and how effective these rates are in generating force. The next two sections deal with these questions.

Speed of isometric contraction

In contrast to the linear relationship between firing rate and isometric force we observed, various non-linearities have been reported during nearly steady-state measurements (see Discussion). Therefore, we wished to determine what effects the speed of an isometric contraction had on the firing rates of single units. Subjects were asked to track triangular wave forms with different cycle times varying from 2 sec (0·5 c/s) to 50 sec (0·02 c/s).

Fig. 4 shows typical results for a single motor unit which was studied using triangular wave forms with three cycle times. Using the standard cycle time (10 sec), the firing rate increased quite linearly with force from its threshold near 600 g to the top of the triangular wave form at 1600 g. However, with shorter cycle times the unit became active earlier and at a higher rate. Only beyond a value of 600 g did the firing rate increase substantially, and then to only slightly higher rates than those reached with the 10 sec cycle times. Thus, a positive curvature (second derivatives > 0) is seen. A tendency for an initial discharge at constant rate, and the resultant positive curvature, was observed for each of the four units studied using wave forms with cycle times of 2 or 3 sec.

A different type of non-linearity was observed with long cycle times. The unit in Fig. 4 became active at a somewhat lower firing rate, and

increased its rate rapidly until a 'plateau' rate was reached (about 15 impulses/sec). A negative curvature (second derivative < 0), such as seen in Fig. 4, was observed in four out of the six units studied with triangles repeating every 20 or 50 sec. This type of non-linearity has been observed in many steady-state experiments (e.g. Bigland & Lippold, 1954; Dasgupta & Simpson, 1962; Clamann, 1970). Interestingly, neither non-linearity was as apparent on the falling phases of the triangular wave forms (Fig. 4B). If brackets indicating the s.e. about the mean values had been included in Fig. 4B, they would have over-lapped considerably for all three repetition rates.
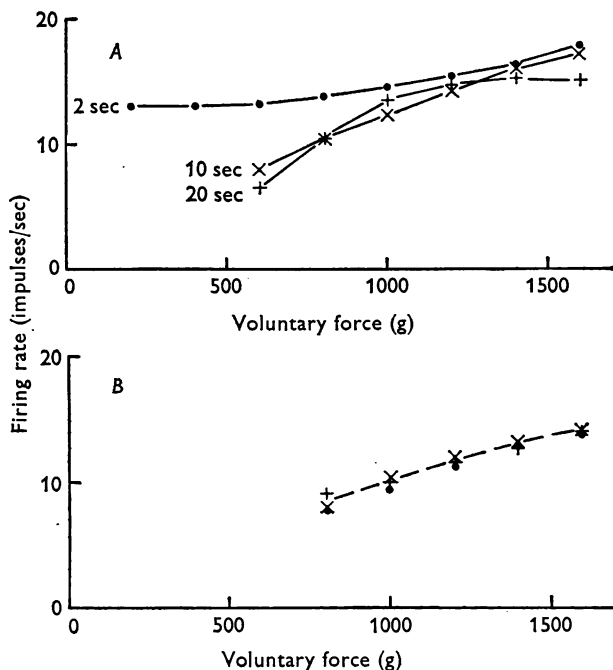

Fig. 4. Mean firing rate of a single motor unit during the rising (A) and falling (B) phases of the voluntary force produced by a subject while tracking triangular wave forms which repeated once every 2, 10 or 20 sec. The non-linearities seen in A with the shortest and longest cycle times are discussed in the text.

Motor units will become active at a lower force level than that at which they become inactive simply due to the fact that the tension must inevitably lag the discharge of the motor unit by 50–150 msec, depending on the time course of contraction. These contractile delays become increasingly significant, the shorter the cycle time. However, the differences observed were often far longer than 50–150 msec, and could also be due to adaptation of the motoneurones (see Discussion). In the sample of 31 units studied, approximately 2/3 ceased firing at a higher force

level than that at which they had become active. Despite the higher force levels on average, 2/3 also fired at a somewhat lower rate just before becoming inactive than their initial rate just after become active (see *Firing rate of motor units*).

Stimulation

To determine the effectiveness of various firing rates in generating force, the first dorsal interosseus muscles of two subjects were stimulated by means of (1) surface electrodes placed over the ulnar nerve, (2) surface electrodes placed directly over the muscle itself, and (3) a bipolar needle electrode (similar to those used for recording) which had been inserted
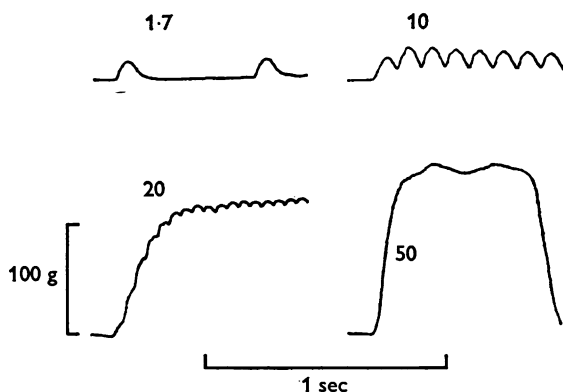

Fig. 5. Tension produced by submaximal stimulation at the rates in c/s indicated. The stimuli were applied through a bipolar needle electrode inserted into the muscle, and the e.m.g. was monitored to ensure that the same number of motor units were being stimulated at each rate.

into the muscle. Maximum voluntary contraction, against a stiff transducer capable of measuring up to 10 kg of tension, produced forces which agreed reasonably well with maximum tetanic stimulation of the ulnar nerve with brief pulses (0·1 msec). The maximum twitch produced by ulnar nerve stimulation was up to twice that generated by direct stimulation of the muscle, which suggests that up to half of the force recorded could have been generated by other muscles. However, direct muscle stimulation using longer pulses (2 msec) proved quite painful even at submaximal levels, so we could never be certain that direct stimulation achieved full activation of the muscle.

Part of the muscle could be stimulated indirectly with little pain by inserting a needle into the muscle (Milner-Brown *et al.* 1973*a*). The needle was manipulated until part of the muscle could be stimulated selectively by a brief stimulus (0·1 msec) and a voltage less than 10 V. The needle was then presumably positioned close to a part of the nerve

supplying the first dorsal interosseus muscle. The voltage was varied until a constant contraction was produced by each stimulus, and then various rates of stimulation were applied. At all times the surface e.m.g. produced by the stimulus was monitored and data were only accepted if the surface e.m.g. did not change in amplitude as the rate of stimulation was varied.

Fig. 5 shows the tension produced by different rates of stimulation applied intramuscularly. At rates up to 10 c/s the tension was relatively unfused. The peak-to-peak fluctuations in tension during the contractions were almost as large with stimulation at 10 c/s as at 1·7 c/s. This provides further evidence for the validity of our measurements of twitch tension
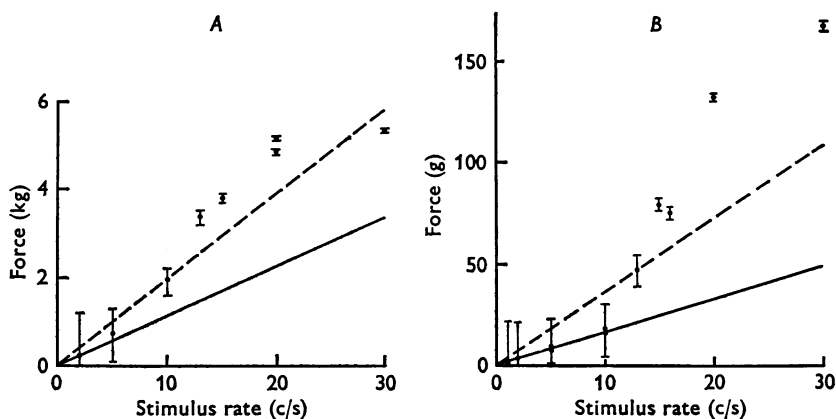

Fig. 6. Force generated by stimulating the ulnar nerve maximally (*A*) or by stimulating intramuscularly through a needle electrode (*B*). The vertical extent of the symbols represents the peak-to-peak fluctuations about the mean values indicated (filled circles). Several rates have been repeated twice. Two linear approximations to the data points (continuous and interrupted lines) are described in the text, although the data appear to lie along a non-linear, sigmoid curve.

and contraction time (Milner-Brown *et al.* 1973*a*) from the maintained discharge of a motor unit evoked voluntarily at rates below 10 impulses/sec. Fig. 5 also shows that the major increase in tension occurs at rates between 10 and 20 c/s with relatively little increase as the response becomes more fused at higher rates of stimulation.

Fig. 6 compares the force produced in a different subject by various rates of maximal stimulation applied to the ulnar nerve (Fig. 6*A*), or submaximal stimulation applied intramuscularly (Fig. 6*B*). In both subjects tested the twitch/tetanus ratio was higher for ulnar stimulation (0·23, 0·19) than for intramuscular stimulation (0·13, 0·12). The sigmoid shapes of the two curves are otherwise similar despite the fact that the

maximal ulnar nerve stimulation produced over 30 times as much force as the intramuscular stimulation via the needle electrode. Sigmoid curves of this type are generally found, although Bigland & Lippold (1954) were able to fit their data from human subjects by a straight line up to 35 or 45 stimuli/sec. These values were close to the maximum firing rates they observed during voluntary contractions. Two linear approximations are shown in Fig. 6. The first (continuous lines) is based on the area under the twitch in g-sec. If the muscle behaved linearly, each stimulus would produce an equal contribution and the force in g at any rate of stimulation could be obtained by multiplying the g-sec generated per stimulus by the number of stimuli/sec. This prediction is only fulfilled for rates up to 5 or 10 stimuli/sec. Above these rates the tension increases considerably faster until the tetanic tension is approached.

The second linear approximation (interrupted lines) assumes that the muscle can be treated as a critically damped second-order system. This has proven to be a good approximation during partially fused contractions for soleus muscle of the cat (Mannard & Stein, 1973) and for the present muscle (Milner-Brown *et al.* 1973 *a*). The force expected can be computed if any two parameters of the twitch are known, e.g. the twitch tension and contraction time (see Appendix). The second approximation appears to give a better fit to the data, but it may overestimate the force due to recruitment (motor units begin to fire at about 8 impules/sec; Milner-Brown *et al.* 1973 *b*) and underestimate the changes due to rate coding over the normal, physiological range (8–20 impulses/sec). This range represents the steepest portion of the sigmoid curves of Fig. 6. The second approximation will be used in the calculations of the next section, because of its simplicity, but the effect of any deviations from this approximation will be discussed (see *Stimulus rate-tension curves*).

Recruitment vs. rate coding

The amount of force generated by the recuitment of previously inactive motor units during an increasing voluntary contraction can be calculated as follows. Let us divide the entire physiological range of forces into a number of segments, and consider the ith segment. We recorded from a number n_i motor units which were recruited in this segment, which spans a range x_i g. These motor units had a mean twitch tension P_i g and a mean contraction time T_i sec. Once recruited they began to discharge at a rate $r = 8.4$ impulses/sec which did not depend significantly on the segment i, (see *Firing rate of motor units*) and did not vary significantly for any of the three subjects. According to the second-order approximation described in the Appendix, the tension–time integral generated by each impulse in a motor unit having a twitch tension P and contraction time T will be

PTe g-sec where e = 2·72, the base of the natural logarithms. Thus, if each unit is recruited with the firing rate r, the total force y_i generated by recruitment of n_i units in the ith segment is given in g by:

$$y_i = n_i(P_i T_i \, \text{e}) \, r$$
$$= 23 n_i P_i T_i. \tag{1}$$

The force produced by increases in firing rate of motor units, which were already active before the increase in voluntary force of x_i g, can also be calculated. Consider the n_j units which were recorded from and which were recruited at a lower threshold in the jth segment. If these units had a mean twitch tension P_j and a contraction time T_j, they will produce an extra force of $n_j P_j T_j$e g for each impulse/sec that their firing rate increases. We reported earlier (*Firing rate of motor units*) that all units increased their firing rate on average by 1·4 impulses/sec per 100 g or $\Delta r/\Delta x = 0·014$ impulses sec^{-1} g^{-1}. This value did not depend significantly on threshold, and no significant differences between subjects were observed. With an increase in force of x_i g the firing rate will increase $x_i \, \Delta r/\Delta x$ impulses/sec. The extra force due to this increased rate in those units recruited in the jth segment will be:

$$z_{ij} = n_j P_j T_j \text{e} x_i \Delta r/\Delta x. \tag{2}$$

The total force in g due to increase in the firing rate of all those units recruited at lower thresholds will be

$$z_i = \sum_{j=1}^{i-1} z_{ij} = \text{e} x_i \Delta r/\Delta x \sum_{j=1}^{i-1} n_j P_j T_j \tag{3}$$
$$= 0·038 x_i \sum_{j=1}^{i-1} n_i P_j T_j.$$

Thus, at each level of voluntary force, the percentage of extra force due to recruitment (e.g. in the ith segment this will be $100y_i/(y_i+z_i)$) and the percentage due to increased firing rate ($100z_i/(y_i+z_i)$) can be computed for the population of units which we recorded from. For all three subjects (Fig. 7A) recruitment only accounted for the bulk of the force at low force levels. Although increasingly large motor units continued to be recruited at high force levels, they were few enough compared to the number of units already active, that the increased firing rate in the previously active motor units produced the bulk of the extra force. Over the range of contractions considered, which was only a fraction of the entire physiological range, increased rate produced about 2/3 and recruitment only about 1/3 of the total force accounted for (the percentages due to recruitment are listed for each subject in Fig. 7A).

By dividing the total force range into segments, the contribution of rate coding was also underestimated to some extent. Since the segments were quite wide (up

to 500 g) at high levels of force, those units which were recruited early in the seg-
ment will have increased their firing rate considerably by the upper limit of the
segment. Even at low force levels with the narrower segments, some rate coding will
occur for each of the many units recruited within a given segment. This rate coding
was not taken into account in calculating the results shown in Fig. 7. Had this been
done, the forces in g due to rate coding would have been increased by about 10 %.

Also shown in Fig. 7*B* are the percentages of the force accounted for by
two mechanisms (i.e. 100 $(y_i + z_i)/x_i$). Note that the percentages are roughly
constant except at the lowest force levels. A variable amount of force,
which was sometimes as much as 100 g, could be exerted simply by pas-
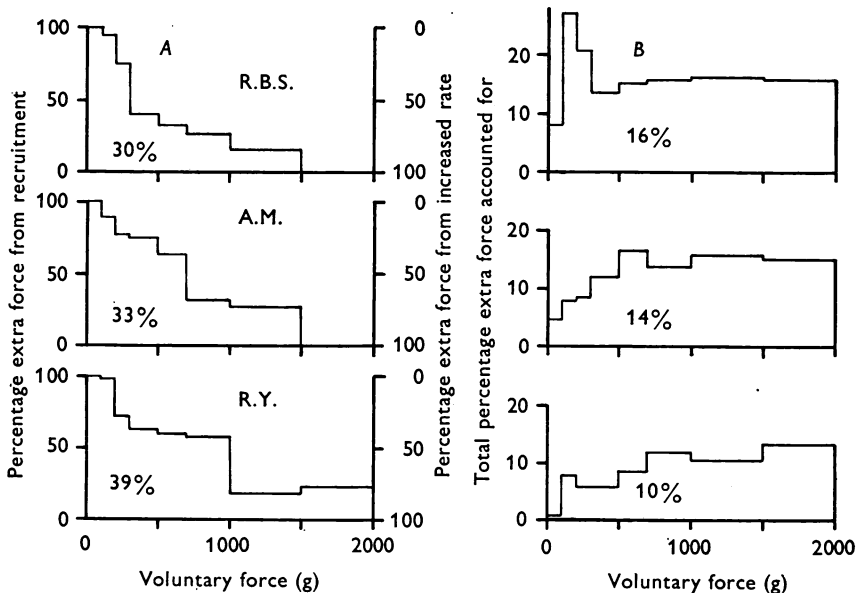sively resting the finger against the transducer. This explains the lower

Fig. 7. *A*, calculated percentages of force due to recruitment and rate coding
for the three subjects at different levels of voluntary contractions. The over-
all percentage due to recruitment for the range studied (0–2 kg) is listed for
each subject. *B*, calculated total percentages of force accounted for by the
units studied at various force levels, considering both the mechanisms
shown in *A*. The percentage accounted for in the entire range studied is also
listed for each subject.

percentages accounted for by active contractile mechanisms at the lowest
force levels. The percentages are always considerably less than 100 %
because only a fraction of the motor units in the muscle were sampled. The
absence of substantial trends in the total percentages of force accounted
for argues against substantial biases in the sample collected. For the three
different subjects the highest percentages were obtained at low (R.B.S.),
medium (A.M.) and high levels of force (R.Y.). The results from the sub-

ject A.M., who was unaware of the purposes of this experiment, fell between those of the other two. Knowledge of the experimental aims probably did not affect the results from the other subjects either, for it was only after completing the experiments and doing the calculations that the results emerged, and they were contrary in many ways to the results expected from our reading of the literature.

DISCUSSION

We have been able for the first time to quantify the forces due to recruitment and the forces due to an increased firing rate of active motor units (rate coding) during increasing voluntary contractions. The results were contrary to the impressions gained from reading the literature. To quote two recent examples, Clamann (1970) concludes that his work, 'quantitifies and expands on the common observation that, at low tension levels, frequency change is the chief means of grading tension, while at higher tension levels, recruitment is the predominant mechanism'. Person & Kudina (1972) state the case rather more flamboyantly, 'Recruitment is undoubtedly the main reserve of contraction strength increase. However, the mechanism of frequency change is unsurpassed as far as precision and smoothness are concerned.' Yet, at low force levels where fine adjustments are made, recruitment proved from our calculations to be the major mechanism. Increased rate proved to be responsible for the coarser adjustments that are made at higher force levels. Considering the whole physiological range, rate coding seems the major mechanism as originally suggested by Adrian & Bronk over forty years ago. Furthermore, our results at the two extremes of tension can be supported virtually without experimentation.

Mechanisms operating during minimal and maximal contractions. In a completely passive muscle, recruitment is the only mechanism operative initially because there are no active units whose firing rate can be increased. Petajan & Philip (1969) measured the 'onset interval' for the first motor unit recorded by a needle electrode and the 'recruitment interval' (i.e. the interspike interval of the first unit occurring when a second motor unit just began to fire). For the first dorsal interosseus muscle, the firing rate increased from roughly 7–10 impulses/sec from onset to recruitment. Increases of 30–35 % were found in many muscles which they termed the 'range of control' by rate coding. How much smaller this range of control by rate coding at low tensions might have been, if Petajan & Philip had considered the difference in interval between onset of the first unit and recruitment of the next unit in the whole muscle, rather than among those few motor units in the region sampled by a needle electrode!

At the other extreme, if all the motor units in a muscle could be activated by nearly maximal voluntary effort, this force could only be increased further by increasing the firing rate of the active motor units (rate coding). Grillner & Udo (1971) (see also Henneman, Somjen & Carpenter, 1965) found that 90 % of the units were already recruited by the time the tension generated in stretching soleus muscle of the decerebrate cat reached 50 % of its final value. From their Fig. 1 it appears that they found no units which were recruited beyond 75 % of the final tension. They attributed much of the extra force to the stiffness enountered when stretching a contracting muscle. However, in our experiments, the muscle was being held at a roughly constant length, but no units were measured in two of our subjects which had thresholds for recruitment between 1·5 and 2·0 kg. In the absence of recruitment, extra force could only come from increased firing rates in active motor units.

Determining the relative importance of the two mechanisms at intermediate levels of force required a considerable amount of experimental work and calculations. Several assumptions and approximations were made at various stages which require further discussion. However, before considering these in detail, it is worth noting that the trend of our results can be deduced simply from the observed linear relations between firing rate and force (Fig. 2).

Firing rate as a function of force. If a straight line were measured which went through the origin (zero intercept), then the rate of firing and the level of contractile force would increase exactly in step beyond threshold. A doubling of rate would occur every time the level of voluntary contraction was doubled. A positive intercept (Fig 2*A*) means that the firing rate will less than double each time the force level is doubled, once threshold has been reached, while a negative intercept (Fig. 2*B*) means that the rate will more than double with a doubling of force. Since the values of intercept decreased continuously (Fig. 3*B*) for units recruited at increasing levels of force, this implies that rate coding should be more important with strong contractions than with weak ones, *even if* the same number of extra motor units had been recruited at each level of force.

Plateaus in firing rate. Many studies (e.g. Bigland & Lippold, 1954; Dasgupta & Simpson, 1962; Clamann, 1970) have reported that the firing rate of motor units reached a plateau as the level of voluntary force was increased slowly. However, Clamann (1970) noted a linear relation between firing rate and force, when subjects tracked triangular wave forms, as found here. Furthermore, using slower and slower wave forms (down to a cycle time of 50 sec), plateaus have been observed (Fig. 4*A*) which become increasingly prominent at the longer cycle times. However, the minimum firing rate also decreased in our experiments, so that the range

of firing rates observed often actually increased with slower contractions and relaxations.

Initial firing at roughly constant rates. With faster cycle times of 2 or 3 sec, motor units fired faster, earlier in the cycle, and initially with a roughly constant rate. Recently Gillies (1972) had subjects track linear ramps up to a final maintained level of force. He observed that motor units would often fire faster during the ramp than during the static portion of the wave form. The units might even stop firing altogether if their static threshold had not been exceeded.

The initially constant rate might be attributed to a balance between increasing drive and motoneuronal adaptation. Since adaptation becomes less and less marked with time (Fuortes & Mantegazzini, 1962), adaptation might also account for the fact that the firing rate during the rising, but not the falling phase of force depended on cycle time (Fig. 4). Whatever the mechanism involved, this initial burst at a higher rate does limit the scope for rate coding, so this mechanism may be relatively less important during rapid contractions. Again, one could argue *a priori* that with the briefest movements, in which motor units only fire once or twice, rate coding can play no part. Very little change in discharge pattern was observed during relaxation (Fig. 4B), with the range of cycle times used.

Sampling bias. The possibility that our samples contained a smaller fraction of the units, which are normally recruited at high force levels, cannot be ruled out. However, this possibility was discussed in detail in the previous paper (Milner-Brown *et al.* 1973b), and reasons were given for thinking that substantial bias was not present in the range of forces studied. Furthermore, no systematic trends were observed in the total percentages of force accounted for by the units studied using the two mechanisms (Fig. 7B). To argue that the forces due to recruitment were substantially underestimated at high force levels, reasons would also have to be given for thinking that the forces due to rate coding had been overestimated at these levels.

Nonetheless, with the number of units sampled (see Table 1 of Milner-Brown *et al.* 1973a), somewhat higher percentages might have been expected at all levels of force. From the percentages listed in Fig. 7B, 200–400 motor units would be required to account for 100% of the force. The only published histological measurements (Feinstein *et al.* 1955) indicated the presence of approximately 200 large axons in the nerve to the first dorsal interosseus muscle, and some of these were presumably Group 1 muscle afferents. This supports our earlier suggestion (*Stimulation*) that other muscles were probably also contributing some force. Other factors could also have affected the absolute values computed. For example, the absolute value of force measured in Fig. 6B at 20 c/s was nearly twice that expected from the linear approximation (interrupted line).

Stimulus rate–tension curves. When stimulating either the whole muscle via its nerve, or a part of it with intramuscular electrodes, a sigmoid

relation was observed (Fig. 6) between tension and stimulus rate, as generally found (Adrian & Bronk, 1929; Cooper & Eccles, 1930; Rack & Westbury, 1969). For simplicity in the calculations, a linear approximation was used, which assumed that the muscle could be treated as a critically damped second-order system.

The predictions from this approximation were larger and fitted the data points in Fig. 6 better than those from an approximation based on the area under a twitch. The reason is that the relaxation phase expected for a critically damped system is slower than actually observed during a twitch. The half-relaxation time for a critically damped second-order system is nearly 70 % greater than the contraction time (see Appendix), while the half-relaxation time of the twitches shown in Fig. 5 is less than the contraction time. However, Mannard & Stein (1973) have shown that repetitive activity at physiological rates slows the relaxation process markedly, and the critically damped approximation holds reasonably well at certain firing rates (see also Milner-Brown *et al.* 1973*a*).

The important point for the present discussion is that the linear second-order approximation appears to overestimate the force due to recruitment and underestimate that due to rate coding (see *Stimulation* and Fig. 6). Thus, any deviations observed will strengthen our conclusions concerning the relative importance of rate coding. The extent of possible errors is uncertain because there were quantitative differences (e.g. in the twitch/tetanus ratio) between the stimulus rate–tension curves with maximal and submaximal (intramuscular) stimulation. The differences may simply result from the submaximal nature of the intramuscular stimulation. Muscle spindle afferents were presumably also being stimulated and at rates of 20 or 30 stimulus/sec could well have activated other motoneurones not directly stimulated by the needle (Upton, McComas & Sica, 1971).

It is also of interest that the common rates of firing we observed (8–20 impulses/sec) agree very well with the range of stimulus rates over which the tension increases rapidly (from roughly 15 to 85 % of its tetanic value). Indeed, the rate coding found during voluntary contractions seems well suited to use nearly the whole range of forces which the muscle can produce. The higher firing rates sometimes observed in other limb muscles (Adrian & Bronk, 1929; Lindley, 1935; Norris & Gasteiger, 1955; Marsden, Meadows & Merton, 1971) would add little to the steady force generated by this muscle.

Maximal voluntary contraction. The forces generated during ulnar nerve stimulation or during maximum voluntary contractions were two to three times as large as the maximum range of forces normally studied (0 to 2 kg) (Milner-Brown *et al.* 1973*b*). If the trends observed in Fig. 7 continued up to maximal voluntary contractions, clearly rate coding would account for considerably more than two-thirds of the total force produced. An upper limit on the total force due to rate coding can be

obtained from the values given above. If by maximal effort all motor units had been recruited and had increased their firing rates from 8 to 20 impulses/sec, then from the stimulation results, the tension due to recruitment would be only $15/85 = 18\%$, rather than the 34% measured on average for our three subjects.

In conclusion, although there are a number of assumptions and approximations which could affect the values calculated, the total contribution of rate coding to the generation of force in this muscle may have been underestimated, rather than overestimated, and the role of recruitment seems mainly confined to the generation of force at the lower levels of voluntary contraction.

APPENDIX

If the tension in response to an impulse in a motor unit can be approximated by the impulse response of a critically damped second-order system (Milner-Brown *et al.* 1973*a*), the tension would be given as a function of time $f(t)$ by

$$f(t) = at\,\mathrm{e}^{-t/T}, \tag{4}$$

where a and T are constants to be determined (Milsum, 1966). Time delays such as occur in excitation-contraction coupling have been ignored. The peak tension occurs when the slope of $f(t)$ against t is 0; i.e. when

$$\mathrm{d}f(t)/\mathrm{d}t = a\,\mathrm{e}^{-t/T}(1-t/T) = 0. \tag{5}$$

Eqn. (5) will obviously hold when $t = T$, so the constant T simply represents the contraction time of the motor unit. The value of the peak tension P can then be obtained by setting $t = T$ in eqn. (4):

$$P = f(T) = aT/\mathrm{e}. \tag{6}$$

From eqns. (4) and (6), half-relaxation will occur when

$$f(t) = aT/(2\mathrm{e}) = at\,\mathrm{e}^{-t/T}$$

or after rearrangement:

$$2\mathrm{e}(t/T)\,\mathrm{e}^{-t/T} = 1.$$

This occurs when $t = 2 \cdot 68T$. Thus, the half-relaxation time should be nearly $1 \cdot 7$ times as long as the contraction time (see discussion of this prediction under *Stimulus rate-tension curves*).

The area under the curve of eqn. (4) (*tension-time integral*) gives the

total number of g-sec contributed by the twitch to the over-all force in the muscle.

$$\int_0^\infty f(t)\, \mathrm{d}t = aT^2 e^{-t/T}(1+t/T)|_\infty^0$$

$$= aT^2 = PT\mathrm{e}. \qquad (7)$$

Eqn. (7) indicates that for this linear approximation, each impulse will produce a contribution of $PT\mathrm{e}$ g-sec, where P is the twitch tension, T is the contraction time, and $\mathrm{e} = 2\cdot72$ is the base of the natural logarithms. This prediction is tested in the text.

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